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REQUIEM—FOR MEGADRILE UTOPIAS. A CONTRIBUTION TOWARD THE UNDERSTANDING OF THE EARTHWORM FAUNA OF NORTH AMERICA[1]

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The origin and constitution of a major portion of the earthworm fauna of America, north of the Mexican border, long have been misunderstood, not only in Europe but also in the western hemisphere. A possibility that greenhouses could provide clarifying evidence was recognized years ago (*cf.* Gates, 1943) when I identified specimens of exotic earthworm species, otherwise unknown locally, that were obtained from wholesale American greenhouses. Investigations of animals in greenhouses of Berlin and Italy (Boettger, 1929, 1930, 1932), Berne, Switzerland (Holzapfel, 1932), Poznan, Poland (Moszynski and Urbanski, 1932) provided some oligochaete records. Other and fortuitous greenhouse records of earthworms, widely scattered through systematic and other literature, are of greater interest. Greenhouse faunas as such never were studied in America. In the fall of 1952, I began collecting in retail greenhouses, mostly in Maine. Some of the data was included in a previous publication (Gates, 1963); the remainder is recorded here. Other material was provided by Harold Davies, Dorothy McKey-Fender, and Professors Harman and Murchie.

All greenhouses mentioned below are heated during cold months and elsewhere often are called forcing houses or hot houses to distinguish them from those that are not heated. Collecting from plant benches usually was inadvisable while plants were growing and was futile after the earth had dried. Records are for groups of buildings rather than for individual

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houses in a set. Unless otherwise indicated, I was the collector. The customary method of indicating megadrile growth stages is by three figures (following the date of collection) which tell the number of juvenile, aclitellate and clitellate specimens, respectively. A fourth number, if mentioned, states the number of postsexual aclitellate individuals. The year of collection often was lacking on the label of the specimens and so cannot be included below.

LUMBRICIDAE

Allolobophora Eisen, 1874

Allolobophora chlorotica (Savigny, 1826)

District of Columbia. Washington, Greenhouses, Poplar Point Nursery, U. S. Botanical Gardens, 5 March 1954, 0–5–1. Collector: W. J. Harman.

Remarks: Other greenhouse records are for New York, Massachusetts, Maine, Finland, Poland, France, Switzerland. *A. chlorotica* is not common in central Maine.

Allolobophora longa Ude, 1885

Maine. Bangor, Bangor Floral Company, soil under plant benches, 22 December, 2–0–0, 7 January, 1–0–0. Sunnyside Greenhouses, soil under plant benches, 28 February 1953, 5(+ 7?)–0–0. Hard earth above stiff clay floor under plant benches, 5 November 1953, 5(+ 27?)–0–0. Lougee-Frederick greenhouses, soil under plant benches, 25–26 November, 1(+ 7?)–0–0. Seavey greenhouses, soil under plant benches, 13 December, 1(+ 8?)–0–1.

Remarks: *A. longa*, recorded from botanical gardens and arboretums of several countries and not uncommon in central Maine, hitherto had not been reported from greenhouses.

Allolobophora trapezoides (Duges, 1828)

Maine. Waterville, Flo's greenhouse, soil under plant benches, 23 June, 12(+ 87?)–0–5–2, 11 August, 17–2–4–7. (At least some of 24 recently hatched juveniles of *Allolobophora* sp., may have been of this species.) District of Columbia. Washington, Greenhouses, Poplar Point nursery, U. S. Botanical Gardens, 5 March 1954, 0–5–1. Collector: W. J. Harman.

Remarks: *A. trapezoides* was previously unrecorded from American greenhouses, probably, in part, because it was confused with other species (*cf.* notes to Table 1). Specimens never were obtained outdoors anywhere in Maine.

Earth on plant benches of the Maine greenhouse had not been changed for 16 years (at least) and at end of each growing season was allowed to dry for 2–3 weeks.

TABLE 1. Presence of European earthworms in greenhouses and in Pacific Coastal states. G–Greenhouses. W–Washington. O–Oregon. C–California. (+) New state record. (?) Present in British Columbia and anticipated in Washington. (H), (E), Holarctic, Euro-american, according to some European specialists.

		G	W	O	C
Allolobophora chlorotica	(E)	+	+	+	(+)
A. limicola	(E)				
A. longa	(E)	+			
A. muldali	(E)				
A. trapezoides		+	(+)	(+)	(+)
A. tuberculata		+	(?)		(+)
A. turgida		+	(+)	(+)	(+)
Dendrobaena mammalis	(E)				
D. octaedra	(E)		+		+
D. rubida	(H)	+	+	+	+
Eisenia foetida	(H)	+	+	+	+
E. hortensis	(E)	(+)		+	+
E. rosea	(H)	+	+	+	+
Eiseniella tetraedra	(H)	+	(?)	+	+
Lumbricus castaneus	(E)	+		+	
L. festivus	(E)				
L. rubellus	(E)	+	+	+	+
L. terrestris	(E)	+	+	+	+
Octolasion cyaneum	(H)	+			(+)
O. tyrtaeum	(H)	+	+	+	+

Notes: *Allolobophora trapezoides, tuberculata, turgida,* along with *nocturna,* and perhaps other unrecognized species, formerly were included in a taxon known as *caliginosa* that was characterized as holarctic. *Octolasion tyrtaeum* formerly was known as *Octolasium lacteum. Eisenia rosea,* by some Europeans, is included in *Allolobophora* but like each of the six species in the table, *limicola* to *turgida,* does not belong in any genus of which *chlorotica* is the type species.

Allolobophora tuberculata Eisen, 1874

MAINE. Bangor: Bangor Floral Company, earth of plant benches, 14 October 0–17–31. Soil under plant benches, 22 December, 30–6–1; 7 January (several small juveniles?)–2–4. Earth of plant benches, 7 March, 9(+ 8?)–1–21–1. Bangor Nursery, earth of plant benches, 14 October, 13–17–31, 20 October, 14–4–4. Lougee-Frederick greenhouses, soil under plant benches, 28 November, 0–0–2. O'Loughlin's greenhouses, soil under plant benches, 28 November, 0–0–2. Seavey's greenhouses, soil under plant benches, 13 December, 6(+ 7?)–3–2–1. Sunnyside greenhouses, hard earth above stiff clay floor under plant benches, 5 November, 2(+ part of 19 smaller juveniles?)–4–3. In earth (brought in the previous fall) of plant bench, 28 February, 0–0–6. In earth under plant benches, 18–20 April, 8–0–0. Bar Harbor: Dorrance greenhouses, soil

under plant benches, 25 May, 4–0–4. Browning greenhouses, soil under plant benches, 25 May, 2–0–1. Malvern Flower Shop, soil under plant benches, 25 May, 2–0–2. McIntosh greenhouses, soil under plant benches and 1–2 inches beneath a layer of coal cinders, 25 May, 5–0–0. Ellsworth: Clark greenhouses, soil under plant benches, 24 March, 63–0–10–2. Orono: University of Maine greenhouses, earth of plant benches, 25 October, 8–2–8. Waterville: Flo's greenhouse, soil under plant benches, 23 July, 0–1–1. 11 August, 4–2–1.

Remarks: Not previously reported from greenhouses. Common throughout central Maine.

Allolobophora turgida Eisen, 1874

Maine. Bangor: Bangor Floral Company, earth of plant benches, 20 October, 0–0–1. Soil under plant benches, 22 December, 0–0–1, 7 January, 0–0–1. Sunnyside greenhouses, hard earth above stiff clay floor under plant benches, 25 November, (some of 19?)–0–4. Soil under plant benches, 18–20 April, 4–2–16 (some in copulation). Bar Harbor: Malvern Flower Shop, soil under plant benches, 25 May, 0–1–1–1. Ellsworth: Clark greenhouses, soil under plant benches, 24 March, 0–0–0–3. Waterville: Flo's Greenhouse, soil under plant benches, 23 July, 0–0–1. 11 August, 0–0–7.

Remarks: Not previously reported from greenhouses. Not as common in central Maine as is *A. tuberculata.*

Dendrobaena Eisen, 1874

Dendrobaena rubida (Savigny, 1826)

Maine. Bangor: Bangor Nursery, earth of plant benches, 14 October, 0–0–3. Bangor Floral Company, earth of plant benches, 20 October, 0–0–3. Soil under plant benches, 7 March, 0–0–6. Lougee-Frederick greenhouses, soil under plant benches, 25 November, 0–1–0. Sunnyside greenhouses, soil under plant benches, 25 November, 0–0–1. Ellsworth: Clark greenhouses, soil under plant benches, 24 March, 4–0–0. Orono: University of Maine greenhouses, earth of plant benches, 25 October, 1–0–2. Waterville: Flo's greenhouse, soil under plant benches, 23 July, 9–3–0. 11 August, 14–13–3–1. Specimens were of athecal morphs.

Connecticut. Greenwich: Compost heap outside the Saxon-Krueger greenhouses, 27 August 1957, 0–1–0. (Compost heap comprised discarded plant materials taken outside.)

Remarks: Most specimens were of thecal morphs known in the past as *D. subrubicunda.*

An additional Maine record, hitherto unpublished, is of some interest in connection with the subsequent discussion. Sandy loam, 4½ feet below ground level, in unfloored cellar of a dwelling house at Benton Station, 15 September 1950, 0–1–0. H. S. Smith.

Outdoors the worm had burrowed down to a level below the foundations which were then tunnelled under so as to come to the surface in-

side the cellar. The species is not usually regarded as one of the deep burrowing forms.

Other greenhouse records are for Finland, Poland, Germany, Switzerland, Italy.

Eisenia Malm, 1877

Eisenia foetida (Savigny, 1826)

Maine. Bangor: O'Loughlin greenhouses, in soil under boards beneath plant benches, 28 November, 2–0–0. Lougee-Frederick greenhouses, soil under plant benches, 25–26 November, 6–0–0. Bangor Floral Company, manured earth of plant benches, 7 March, 1–0–2. Bar Harbor: Dorrance greenhouses, soil under plant benches, 25 May, 1–0–0. Malvern Flower Shop, manured earth of plant benches and in soil underneath benches, 25 May, 16–9–6. Ellsworth: Clark greenhouses, soil under plant benches, 25 March, 4–2–0.

Remarks: Other greenhouse records are for Illinois, Maryland, Massachusetts, Sweden, Poland, Germany, Wales.

E. foetida is widely distributed in central Maine but, in any township, provides only a small proportion of the megadrile population because of drastic ecological restrictions.

Eisenia hortensis (Michaelsen, 1890)

Michigan. Masury, Trumbull County, 0–0–2. Collector: W. R. Murchie.

Remarks: Previously recorded from a greenhouse and a conservatory in Maine as well as from a hot bed with a temperature of 80–85° F at Ardsley, New York. Another of the very few North American reports was for a toilet bowl in Cleveland.

Eisenia rosea (Savigny, 1826)

Maine. Bangor: Bangor Floral Company, earth of plant benches, 14 October, 0–0–2, soil under plant benches, 22 December, 0–0–1, 7 January, 1–0–3, 7 March, 2–5–10–3. Sunnyside greenhouses, hard earth above stiff clay floor under plant benches, 5 November, 0–0–5, 28 February, 0–0–3. Lougee-Frederick greenhouses, 25–26 November, 0–0–8. Seavey greenhouses, soil under plant benches, 13 December, 6–1–2. Bar Harbor: Dorrance greenhouses, soil under plant benches, 25 May, 8–1–2. Browning greenhouses, soil under plant benches, 4–0–0. Ellsworth: Clark greenhouses, soil under plant benches, 24 March, 10–4–16–3. Orono: University of Maine greenhouses, in earth of plant benches, 25 October, 0–0–1. Waterville: Flo's greenhouse, soil under plant benches, 23 July, 2–0–2.

Remarks: Other greenhouse records are for Oklahoma and Italy. *E. rosea* is common outdoors throughout central Maine.

Eiseniella Michaelsen, 1900

Eiseniella tetraedra (Savigny, 1826)

Maine. Ellsworth: Clark greenhouses, soil under plant benches, 24 March, 0–0–4. Waterville: Flo's greenhouse, soil under plant benches, 23 July, 46–2–4. 11 August, 9–2–4. District of Columbia. Washington: Greenhouses, Poplar Point nursery, U. S. Botanical Gardens, 5 March 1954, 0–0–4. Collector: W. J. Harman.

Remarks: All specimens were of morphs with male pores in xiii. *E. tetraedra* is fairly widely distributed in central Maine but is present at few sites, three of which are in Bangor and vicinity.

Other greenhouse records are for Indiana and Finland.

Lumbricus Linnaeus

Lumbricus castaneus (Savigny, 1826)

Maine. Bangor: Lougee-Frederick greenhouses, soil under plant benches, 25–26 November, 1–0–0. Bangor Floral Company, earth of plant benches, 7 March, 0–1–2. Orono: University of Maine greenhouses, earth of plant benches, 25 October, 2–0–0.

Remarks: Other greenhouse records are for Finland and Poland. *L. castaneus* is fairly common throughout central Maine.

Lumbricus rubellus (Hoffmeister, 1843)

District of Columbia. Washington: Greenhouses, Poplar Point nursery, U. S. Botanical Gardens, 5 March 1954, 0–1–2. Collector: W. J. Harman. Oregon. Dayton: Greenhouse, 14 July 1946, 0–1–29. Collector: D. McKey-Fender.

Remarks: Other greenhouse records are for Poland and Italy.

The species is rare in central Maine where, during a twenty-year survey, only 53 specimens were secured outdoors.

Lumbricus sp.

Maine. Waterville: Flo's greenhouse, soil under plant benches, 23 July, 1–0–0. (Probably not *terrestris*. Identification impossible because a portion of the tail was lacking and the anterior region was damaged.)

Lumbricus terrestris Linnaeus

Maine. Bangor: Bangor Floral Company, soil under plant benches, 22 December, 3–0–0, 7 March, 1–0–0. Sunnyside greenhouses, hard earth above stiff clay floor under plant benches, 5 December, 2–0–0. Lougee-Frederick greenhouses, soil under plant benches, 25–26 November, 4–0–0. Seavey Greenhouses, soil under plant benches, 13 December, 1–0–0. Bar Harbor: Dorrance greenhouses, soil under plant benches, 25 May, 0–1–1. (Specimens also were present in earth of the plant benches.)

Remarks: Except in one house, all specimens were juvenile and quite small.

Other greenhouse records are for Indiana, Illinois, and Switzerland. *L. terrestris* is widely distributed and common in central Maine.

Octolasion Oerley, 1885

Octolasion cyaneum (Savigny, 1826)

Maine. Bangor: Bangor Floral Company, earth of plant benches, 14 October, 0–1–1, soil under plant benches, 7 January, 9–0–0. Bangor Nursery, earth of plant benches, 14 October, 0–1–1.

Remarks: In central Maine this species was found only at six other sites two of which were flower beds outside the greenhouses.

The only other greenhouse record is for Finland.

Octolasion tyrtaeum (Savigny, 1826)

Connecticut. Greenwich: Compost heap outside Saxon-Krueger greenhouses, 26 August, 1957, 0–0–1.

Remarks: *O. tyrtaeum* is rare in central Maine where it was not found in greenhouses.

The only previous greenhouse record was for Naples, Italy.

MEGASCOLECIDAE

Pheretima Kinberg, 1866

Pheretima agrestis (Goto and Hatai, 1899)

Maine. Waterville: Flo's greenhouse, soil under plant benches, 11 August, 0–0–2.

Remarks: This is the first record of the species from a greenhouse.

Pheretima diffringens (Baird, 1869)

New Jersey. Chatham, greenhouses, August 1954, 0–4–9. Collector: H. Davies.

Remarks: Types of this oriental species were secured from an orchid bed in a Welsh "plant stove." Similar worms had been present in an English hot house since 1849. Subsequently the species was reported from greenhouses in France (1870, 1871), Denmark (1886), Scotland (1890), Germany (1892), Russia (1896), Illinois (1915), Poland (1933), Oregon (1936), and Maine (1963). *P. diffringens* probably was the, or one of the, species present as early as 1888 in Illinois greenhouses.

The single record for Nebraska was, from soil in the vicinity of greenhouses. Outdoors in Europe, *P. diffringens* has been found in gardens around greenhouses of France, Portugal and Italy. In America, the species has been collected outdoors in California, Texas, Arkansas, Louisiana, Tennessee, Mississippi, Alabama, Florida, Georgia, South Carolina, North Carolina, Virginia, Pennsylvania, New Jersey, New York, Connecticut, Mexico, Guatemala, Salvador, Costa Rica, and Panama. Recorded sites in Connecticut, New York, New Jersey and Pennsylvania are few, but in many of the other states the species is more widely distributed.

Other colonizations: In Americas, San Domingo, Trinidad, Colombia,

Peru, Brazil. In the other hemisphere, Sardinia, Azores, Egypt, Anjouan, Cape Verde Islands, St. Thomas, St. Helena, South Africa, Madagascar, Ceylon, India, Burma, Sumatra, Java, Philippines, Australia, New Caledonia, New Zealand, Fiji and Hawaiian Islands. The species is widely distributed in Hainan, Taiwan, China, Korea, and Japan. In some portion of the latter area it's original home is to be sought.

Pheretima hilgendorfi (Michaelsen, 1892)

Connecticut. Greenwich: Compost heap outside Saxon-Krueger greenhouses, 26 August 1957, 0–0–6, 28 October 1957, 0–0–3. (*cf.* record for *D. rubida.*)

Remarks: Earthworms could not be collected in the greenhouses but the species probably was taken out to, rather than in from, the compost heap.

Pheretima levis (Goto and Hatai, 1899)

Connecticut. Greenwich: Compost heap outside Saxon-Krueger greenhouses, 26 August 1957, 0–0–7, 28 October 1957, 0–0–19.

Remarks: Earthworms could not be collected in the greenhouses but the species probably was taken out to, rather than in from, the compost heap.

Pheretima morrisi (Beddard, 1892)

Michigan. Campus greenhouse, Flint College, Genesee County, 20 February 1961, 0–0–9. Collector: W. R. Murchie.

Remarks: Previous greenhouse records are for Bangor, Maine, Poughkeepsie, New York, and England.

Discussion

A twenty-year survey of the megadrile fauna of central Maine, involving identification of thousands of earthworms, showed presence outdoors only of lumbricids belonging to 14 species. Eleven of them were found in greenhouses. *Dendrobaena octaedra*, *Lumbricus rubellus*, and *Octolasion tyrtaeum* were secured at very few sites and then only in habitats from which the taking of soil to local greenhouses is unlikely. Two of those species have been found in greenhouses elsewhere and there is very good reason (to be presented subsequently) for believing that *Dendrobaena octaedra* would have been found indoors long ago, if more than a few searches had been made.

Greenhouses and conservatories in which plants were raised only from seeds and/or bulbs usually harbored no foreign worms, *i.e.*, of species absent outdoors in the same region. Earthworms of those buildings probably arrived with the earth for the plant benches. However, deep burrowing species, such as *Allolobophora longa*, *Lumbricus terrestris*, *et al.*, could have gotten in by tunneling under the foundations as floors are lacking.

On several occasions earthworms actually were found in the animal manure and/or compost that was being taken inside as fertilizer. Co-

coons were not sought but probably would have been present in almost all of the bench materials that went into Maine greenhouses. Once inside, the worms spread to the more or less undisturbed soil of the floorless areas and to odd corners or niches where dirt or accumulations of plant matter provide appropriate shelter, food and moisture. Bench earth of one greenhouse had not been changed for at least 17 years, but had been allowed to dry out for a short period before being again put to use. A much more usual practice was to discard the earth at the end of a growing season, or at various intervals ranging from one to several years, and then to refill the benches with fresh earth from some supposedly favorable site. Cocoons, or perhaps less often diapausing individuals, could have remained behind even in crannies of the wooden benches which in the past were not sterilized. Indeed, *Allolobophora chlorotica* was found so often inside greenhouses and so rarely outdoors as to lead to a belief that in Maine (and perhaps also in some other New England states) more individuals of the species were taken out than were brought in.

The numbers of specimens obtained, even in small areas of some greenhouses, and the condition of the individuals in comparison with that of worms of the same species from mines, caves, and various outdoor sites, seemed to indicate that the ivied aisles of greenhouses generally provided for earthworms of several species a habitat that was optimal with regard to moisture, temperature, and food, as well as shelter from many enemies. Indeed, that seems to have been learned by Englishmen well over a hundred years ago (*cf.* Baird, 1869) as was proved by complaints that pheretimas had become so numerous in their greenhouses as to block the drains. Perhaps long ago, marked increases in the number of foreign megadriles was found to be one good reason for frequent changing of earth in plant benches. Accordingly, even a small business or private hobby may provide opportunity for rapid multiplication and subsequent distribution throughout a local area of foreign earthworms. An instance of the beginning of one such distribution was detected recently (Karppinen and Nurminen, 1964) in Finland—the spreading of *O. cyaneum*, otherwise unknown in the country, from a local greenhouse first to one garden and then to others in the same area.

Some small organizations purchase, perhaps more often now than in the past, partly or fully grown plants from wholesale businesses. If buildings of the much larger concerns are infected with earthworms, a rapid and widespread distribution of megadriles therefrom would seem to be possible. Wholesale houses that were investigated in the thirties and early forties were indeed sheltering foreign earthworms.

Central Maine greenhouses were found to harbor nine foreign species that are present outdoors only at varying distances beyond the state. *Pheretima agrestis*, for example, is present in the Arnold Arboretum of Boston (Gates, 1953), and beyond that not until Greenwich (Connecticut), Long Island (New York), and Swarthmore (Pennsylvania).

In contrast, *P. bicincta* has been collected outdoors in this hemisphere only in the West Indies.

The self-acquired range of the genus *Pheretima* (Gates, in press) is comprised of: the Andaman Islands, the mainland of Asia from the Chindwin-Irrawaddy axis of Burma east through Yunnan and Szechuan provinces of China to include Korea and Japan, then south through New Guinea, Java, and Sumatra. Salt water usually is believed to be fatal to earthworms which are therefore unlikely to migrate overseas. During the present century no one has suggested seriously that extra-oriental distributions of pheretimas were achieved other than by fortuitous transportation. The only agent definitely known to have engaged in such transoceanic carriage, for the most part unintentionally, is man. Ten species of *Pheretima* have been recorded from the mainland United States where distributions, each marked by wide discontinuities often involving geographical barriers, are fortuitous and indicative of rather recent introduction. Each species now has been reported from American greenhouses or (two species) from the immediate vicinity of such buildings, out of which the worms probably were taken. In greenhouses, pheretimas are known to have survived demolition of the superstructure by fire (Gates, 1963), removal of all earth from plant benches, and drouth of several weeks duration. Once well established indoors, some species are known to have existed without recruitment from outside for periods of 17 to 25 years. Discarding the earth from plant benches, whether annually or at less frequent intervals, often must have resulted in massive innoculations of various age stages, as well as of cocoons, into whatever area the discarded earth was dumped. Certainly, for more than a century, pheretimas went out of European greenhouses in greater numbers then went inside. Yet, in spite of all such transfers, none of the species has been recorded from outdoor sites in Wales, England, Scotland, Denmark, Poland, Germany, Russia, or even in Maine where they must have been present in some greenhouses as long ago as 1920. All of the data subsequently secured, supports the conclusion (Gates, 1963) that greenhouses, in certain parts of the world, have provided centers for introduction, multiplication and local distribution of exotic earthworms originally from China, Japan.

Absence of pheretimas from Maine to Russia, after more than a century of repeated introductions and inoculations, indicates that the species involved cannot survive in those places. Climatic factors presumably are responsible, and temperature seems especially important.

The twenty lumbricid species of Table 1 originated in a western portion of the Eurasian land mass and that origin never has been questioned. However, there are differences of opinion as to the adjectives by which each of those worms are characterized. Holarctic and Euro-american (*cf.* Omodeo, 1963, *et al.*) are the terms used by some Europeans. Holarctic seems more likely to convey an erroneous idea than to communicate information about two species of *Octolasion* that are unrecorded from Alaska, Canada, and Greenland. *Eisenia foetida* once was recorded

from Vancouver and once was said (without mention of localities) to be present in one or more of the eastern provinces, but since has not been reported from any part of Canada, nor from Alaska and Greenland. The only Canadian record for *E. rosea* is that of an Ontario bog not far from the United States boundary. *Allolobophora caliginosa*, also supposedly Holarctic, was a long-used name for a complex containing *Allolobophora nocturna*, *trapezoides*, *tuberculata*, *turgida*, and possibly other unrecognized species. The original home of *nocturna* is unknown *Allolobophora trapezoides* may have evolved in a region with a mediterranean climate and so is unlikely to be found in most of Canada. Holarctic is, of course, much more applicable to *Dendrobaena rubida* and *Eiseniella tetraedra*, but does not hint at the presence of both species in Mexico, Central and South America, Australia, New Zealand, South Africa, and many oceanic islands.

Data that should be noted about so-called Euro-american species are as follows: *Allolobophora muldali* is known only from three sites, in Michigan, Wales, and England. *Dendrobaena mammalis* has been found only once outside Europe (including the British Isles) and then at a single New Jersey site. *Lumbricus festivus* was thought to be present in one or more eastern provinces of Canada (but as yet without confirmation) and the literature provides no support for its supposed presence in the Alleghanies. In the American hemisphere, *Allolobophora limicola* has been found only at the Arnold Arboretum in Boston and at three sites in New Jersey. *Eisenia hortensis*, though recorded from eight states, is encountered but rarely and never was reported from Alaska, Canada, and Greenland.

Allolobophora longa and *Lumbricus terrestris*, on the basis of published distributions, would seem to be much more entitled to a holarctic characterization than *Eisenia foetida* and the two species of *Octolasion*. The same sort of data provides no obvious reason for excluding *Allolobophora chlorotica*, *Dendrobaena octaedra*, *Lumbricus castaneus* from a group containing *Dendrobaena rubida* and *Eiseniella tetraedra*. A characterization of Euro-american gives no hint as to presence elsewhere of the following species: *Allolobophora chlorotica*, in New Zealand, South America, various oceanic islands. *A. longa*, Australia, New Zealand, South Africa. *Eisenia hortensis*, South America, South Africa, oceanic islands such as the Azores. *Lumbricus rubellus*, New Zealand, South Africa, oceanic islands such as Tristan da Cunha; *Lumbricus terrestris*, Australia, New Zealand, South America, South Africa, oceanic islands such as the Azores and Madeira. Anthropochores of European origin, seems to be the most meaningful characterization of the species in Table 1.

American zoologists are apt to regard common European forms with which they long have been more or less familiar, perhaps since boyhood angling days, as native species. For example, *Lumbricus rubellus*, present at almost every location in Washington west of the Cascades where any earthworms are found (Altman, 1936), was said to be "our most common

endemic earthworm." Unfamiliar pheretimas, when encountered occasionally, on the contrary, are assumed by almost everyone to be exotic.

Divergence of opinion on the above-mentioned characterizations of earthworm species doubtless results from different beliefs as to time of arrival in America of species that admittedly are of European origin. My view, first expressed in print more than three decades ago (Gates, 1929a,b), is that "In a large portion of the glaciated area of North America we can not, of course, expect to find indigenous species of earthworms. This part of the continent is inhabited by peregrine lumbricids presumably introduced by man." The same belief more recently (Gates, 1960) was restated with reference to that part of the continent north of Mexico and east of the Pacific coastal strip, "37 (over 60%) of the species in the area now under consideration became domiciled more or less widely after introduction by man." No date was mentioned but another article (Gates, 1954) did say that European lumbricids "probably have been established in the United States for 150 years or more." Some ornithologists were, and still may be, stymied by the problem of the woodcock's diet if there were no earthworms in New England and Canada until some time after 1500 A. D. But, was the preColumbian range of the woodcock the same as now? Furthermore, if the Colorado potato beetle abandoned the deadly night shade for the more nutritious potato in vast plantings, might not a change to a more luscious diet be possible for the woodcock?

Centuries are far from sufficient, according to Omodeo (1963), who presented to a recent symposium on North Atlantic Biota, indirect proofs, inductive arguments, data from biometric and caryological studies, as well as very convincing direct proofs that there is "only one explanation for the type of distribution we are dealing with, the existence of a landbridge across the North Atlantic along which the earthworm fauna of Europe moved to North America." That involved, according to the same author, a species age of 38–50 million years for *Lumbricus terrestris* and its presence in North America for a million years, also the survival of European lumbricids in Greenland and Iceland during "all of the Last Glacial and maybe the entire Quaternary."

Until geologists do find evidence supporting existence of a north Atlantic bridge at the proper time (*cf.* Wright and Frey, 1965, p. 620, etc.) Occam presumably would favor postulating, in place of migration, transportation. Carriage not only is now assumed for the remainder of this discussion, but carriage solely by man. No other agent has been shown to take earthworms around the entire world as man obviously has done. The most likely way, probably the most common one, by which megadriles were transported is in earth around roots of live plants.

The questions next requiring answers are: How long has man (presumably European) been bringing European earthworms to North America along with live plants, and is such a period of time adequate?

Columbus took live plants to Hispaniola on his second transatlantic voyage, but faunas of the West Indies, Mexico and Central America need

no consideration here. Celts, from one place or another, may have settled beyond the Orkneys to escape the Vikings, as the latter did believe, but records are lacking. Norse sagas relating the colonization of Iceland and Greenland, as well as the futile attempt to settle Vineland (probably a southeastern peninsula of Newfoundland), provide no data on plant carriage. Laborious and usually unrewarding searches of various sources, on the contrary, provided some more or less definite seventeenth century dates, for trees brought to the Atlantic colonies (excepting the French in Canada), in tubs or boxes with earth around their roots: 1611 to 1612, vines and orange trees to Virginia (but from the West Indies). Probably after 1681, plants sent to Pennsylvania by Wm. Penn. About 1647, Peter Stuyvesant's pear tree to New Amsterdam, New York; 1638, Pearmain apple to Charter Oak Place; before 1650, Wyllis' apple to Hartford and Tryan's Pearmain to Weathersfield, Connecticut; 1630, Governor Winthrop's pear tree (Boston?); 1640, Governor's Prince's pear to Cape Cod; about 1643, a Bergamot pear to Roxbury. All these localities are in Massachusetts. Before 1670, an apple tree was taken to Gorgeana (now York), Maine. Other records probably can be provided by further literature searches. (Most of the just mentioned records now may be found in Hedrick, 1950.) Although occasional importation by more prosperous colonists of one or more trees obviously could, and probably did, bring earthworms to the United States, objections may be raised that the present distributions could not have been so obtained.

Greenhouses, as already indicated, might have permitted rapid multiplication, and then more rapid and wider distribution. A history of the greenhouse business, so far as could be ascertained, remains to be written, but among data secured from various sources the following (also *cf.* Hedrick, 1950) are cited.

The first greenhouse in New England was built between 1707 and 1737. A little later, a second, also in Boston, was erected. A greenhouse with orange trees was known to have been in Williamsburg, Virginia, about 1737. The New York Mercury of 2 October 1758, contained the advertisement of a "surveyor who designs "Greenhouses. . . . .with winding funnels through the Wall, so as to keep them warm." Greenhouses seem to have been common in the Philadelphia region around 1760 when Bartram got stone to build his own. Robert Morris had hothouses for orange, pineapple and other tropical plants at one of his estates. A greenhouse is known to have been in New York City during 1764 and shortly afterwards, there were many others, some of them conservatories of estates on the east bank of the Hudson. An extensive conservatory and "two species of hothouses" had a frontage of 180 feet in the Elgin Bontanic Garden, on land, part of which now contains the Rockefeller center, New York City, in 1805. During 1825–1860, wealthy estates in Tennessee and Kentucky had greenhouses. The Belmont mansion, near Nashville had three buildings each 300 feet long for camellias, grapes, tropical fruits. Even in Maine, with a climate unfavorable to civilization according to Toynbee (1935), greenhouse plants were

on sale shortly after 1841. At Bangor, then almost on the very frontier, Sekenger's business, begun in 1850, expanded until in 1899 there were 11 greenhouses each 50 feet long in addition to three, each of which was 100 feet long.

Floral business, during the 1930s, was believed to have become one of the leading industries in the United States. The number of square feet under greenhouse glass, according to the U. S. Census of Agriculture for 1959, was 178,500,370 in 1929, 191,400,495 in 1949, 227, 674,395 in 1959. Those figures do not include private conservatories, farms or businesses with annual receipts from horticultural products of less than $2,000. Even in Toynbee's climatically unfavorable Maine, the greenhouse area for 1959 was 1,080,683 sq. ft. During 1929, there were sold in the United States alone, from greenhouses, nearly 122 million potted plants. At that time, many if not most of the thousands of greenhouses (some present in every one of the 48 states) are likely to have sheltered earthworms. One successful establishment outdoors of a single species per greenhouse per annum theoretically could have resulted, after a few years, in colonization of almost every inhabited continental portion of the entire country. European species, that supposedly came to this continent along a North Atlantic bridge are unlikely to have continued westward so as eventually to climb the continental divide and cross the more western mountain ranges. Those species are more likely to have been taken to the Pacific coastal areas of three states and a Canadian province (*cf.* Table 1) in the same way as they were taken to South Africa, South America, Australia, and New Zealand, *i.e.*, along with live plants.

During the last few years (perhaps five or more), searches through greenhouses of organizations in or near large cities revealed no trace of earthworms. Steam and chemical sterilization, replacement of natural earth by sand, gravel, cinders, etc., feeding plants by nutrient solutions, solid floors, perhaps also other newer practices, had exterminated species that may have been present in the past, and presumably will keep earthworms out of the buildings in the future. Hence, the title of this contribution. However, in smaller businesses, away from very large cities, long continued practices are likely to be less rapidly modified or abandoned. From European greenhouses, zoologists easily secured live specimens, otherwise unobtainable, of exotic species for studies of anatomy, physiology, cytology, as well as of various protozoan and nematode parasites. For such studies some exotic megadriles decreasingly will be available to American zoologists and with the disappearance of the last greenhouse worms there also may have been lost opportunities to secure pertinent data as to arrival here of species such as *Dendrobaena mammalis* and *Allolobophora muldali.*

Summary

Data now available in print show that exotic species of non-lumbricid earthworm families transported around the world in earth surrounding roots of live plants could have been propagated in the favorable environ-

ment provided by greenhouses from whence the worms could have been distributed more or less widely in accordance with sales patterns of potted plants. Colonization presumably is allowed or inhibited by climatic conditions in accordance with genetically determined tolerances. Lumbricid species, admittedly of European origin, could have been brought intermittently to the United States along with live plants during the last 355 years. For 250 years, some, perhaps many of those twenty kinds, could have been propagated in American greenhouses. From thence the worms could have been distributed outdoors on a gradually increasing scale. The growth of retail and wholesale horticultural businesses in the country has been such as to warrant a belief that it could have been responsible for a considerable portion of the distributions of the European species as now known.

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